MOVING TOWARDS A STRATEGY FOR ADDRESSING CLIMATE DISPLACEMENT OF MARINE RESOURCES: A PROOF-OF-CONCEPT

*Running title: Climate-informed management in a changing sea*

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**Abstract**

Realistic predictions of climate change effects on natural resources are central to adaptation policies that try to reduce these impacts. However, most current forecasting approaches do not incorporate species-specific, process-based biological information, which limits their ability to inform actionable strategies. Mechanistic approaches, incorporating quantitative information on functional traits, can potentially predict species-specific responses resulting from the cumulative impacts of small-scale processes acting at the organismal level, and can be used to infer population-level dynamics and inform natural resources management.

Here we present a proof-of-concept study using the European anchovy as a model species that shows how a trait-based, mechanistic species distribution model can be used to explore the vulnerability of marine species to environmental changes, producing quantities-based outputs useful when informing fisheries management. We crossed scenarios of temperature and food to generate quantitative maps of selected mechanistic model outcomes (*e.g.* Maximum Length and Total Reproductive Output).

These results highlight changing patterns of source and sink spawning areas as well as the incidence of reproductive failure. This study demonstrates that model predictions based on functional traits can reduce the degree of uncertainty when forecasting future trends of fish stocks. Such a sensitive and spatially-explicit predictive approach may be used to inform more effective adaptive management strategies of resources in novel climatic conditions.

*Key-words:*Climate change, Dynamic Energy Budget model, *Engraulis encrasicolus*, temperature increase, life-history traits, scenarios, climate-informed management

**Introduction**

Understanding and forecasting how ongoing climate change will likely alter the structure and functioning of ecosystems is one of the central challenges facing marine environmental managers (van de Pol et al. 2018). This task is especially challenging due to the high levels of spatial and temporal heterogeneity in climate- and non-climate-related drivers (Lohrer et al. 2015), the interaction of multiple stressors on organisms and ecosystems (Crain et al. 2008) and high variability in the vulnerability of different species to environmental change (Gunderson et al. 2016).

Specifically, whilst climate change is a global phenomenon, species respond physiologically and behaviourally to local environmental conditions (Helmuth et al. 2014). Scaling up responses to forecast future responses of ecosystems and their component species requires an understanding of how key drivers will individually and collectively affect ecosystem composition, structure and function at local scales; however, large gaps still exist in our basic knowledge of most marine species (Fulton 2011; Pecl et al. 2014; 2017). Moreover, organisms are increasingly likely to experience novel suites of environmental conditions, and so their responses are also likely to be novel and difficult to predict (Solow 2017; van de Pol et al. 2018). As a consequence, we need new tools that, whilst being informed by knowledge of current distribution patterns, can also account for organisms’ vulnerability to a broader range of conditions than those currently or previously observed.

To improve projections of the future status of individual species and ecosystems, and to effectively support the development of more sustainable policies that minimize expected impacts and maximize potential opportunities, as in the case of fisheries management, novel combinations of modeling and field and laboratory experimentation are recommended (Korell et al. 2019). Such an integrated approach is necessary to produce realistic forecasts at spatio-temporal scales relevant to organisms and populations (Burrows et al. 2011; Helmuth et al. 2014, Pacifici et al. 2015; van de Pol et al. 2018; Queirós et al., 2018). While several existing predictive ecological modelling frameworks produce model outputs and scenarios with different fields of application depending on the question being addressed, primarily dealing with biodiversity and conservation management context (Koenigstein et al. 2016), each have distinct strengths and weaknesses.

*Predictive ecological modeling frameworks to management:* *the mechanistic model*.

The adoption of a risk-based approach and of process-based (hereafter mechanistic) models has been recently suggested as a way to improve such predictions (Pecl et al. 2014; Pacifici et al. 2015; Goh et al. 2017). By using functional trait-based mechanistic bioenergetics (*sensu* Kooijman 2010; Sousa et al. 2008; 2010; Sarà et al. 2013; 2018) coming from experimental data, mechanistic models are able to incorporate the effects of environmental drivers at levels that exceed the range of values currently operating in nature (Teal et al. 2018). The spatially- and temporally-explicit quantitative predictions generated by these models are species-specific and based on life-history traits such as body size and fecundity (Pecquerie et al. 2009; Kearney et al. 2010; Pethybridge et al. 2013). Model outcomes such as these are critical to parameterize population-based models and are required if they are used to inform appropriate, proactive mitigation and adaptation strategies at scales relevant to spatial management and national and regional policy decision-making (van de Pol 2018; Sarà et al. 2018; Mangano et al. 2019). As a drawback, mechanistic models are more time-consuming to develop, as they require detailed information on species-specific dynamic responses to environmental change (Fennell et al. 2013). To date, however, relatively few examples exist of the application of such approaches over large geographic scales (Montalto et al. 2016) and they are seldom applied to commercially important species (Sarà et al. 2018, Mangano et al. 2019).

*Future proofing marine resource management: a case study using Engraulis encrasicolus.* One of the most critical issues when designing effective marine resources management strategies and plans is represented by trade-offs among fisheries or between fisheries and other management objectives, such as conservation. This can be exemplified by the European anchovy (*Engraulis encrasicolus*) case study. Management objectives, and the relative efficacy of different approaches, may consider not only the stock availability for fisheries (*i.e.* the economic role), but also the biomass available to sustain natural predators and species persistence through time (*i.e.* the ecological role). Clearly there is an important contribution offered by mechanistic approaches to increase predictive capability with respect to where and when fish stocks will become more vulnerable to collapse, serving as a sensitive, geographically-explicit, early-warning system (Teal et al. 2018; Sarà et al. 2018, Mangano et al. 2019). For policy-makers it would be exceptionally difficult, if not impossible, to accurately generate climate-proof economies, dependent upon exploitable marine resources, without accounting for changes in the environment in which a stock/natural population occurs. These cannot be based on global trends such as increases in global temperature and even regional models may be insufficient unless they consider the coincidence of multiple drivers interacting on local scales (*e.g.* Kroeker et al. 2016). Often these drivers are manifest as mosaics rather than as geographic gradients (*e.g.* Helmuth et al. 2006), making the application of spatially-explicit models increasingly important.

Day by day growing applications of Dynamic Energy Budget (DEB) theory with a particular focus toward fish biology led to the development of species-specific models studying the effects of environmental changes on species life-history traits (Jusup and Matsuda 2015). In this proof-of-concept modelling exercise, we explore a mechanistic physiological approach, based on DEB theory (Kooijman 2010), focus on application to marine natural resource (specifically, fisheries) management, to quantify the effects of future environmental change on the potential distribution and vulnerability of the European anchovy population. By translating environmental change into biological effects through at a fine spatial scale approach, we compared the current status of this population in a core area of the Mediterranean distributional range (*i.e.* the Strait of Sicily, Southern Mediterranean Sea, recognized hotspot for this species; Basilone et al. 2006) with its future responses to predicted temperature increases. A sensitivity analysis to simulate both temperature increase and trophic condition scenarios (food availability, *i.e.* oligo- and eutrophic conditions) allowed us to explore the robustness of the models’ outputs (Pecquerie et al. 2009; Payne et al. 2015; Kleisner et al., 2017; Sarà et al. 2018).

We developed scenario-specific quantitative maps to show the different simulation outcomes, which allowed: *(1)* the identification of current source and sink areas and the detection of future temporal and spatial shifts and *(2)* the predictions of size-structure shifts and reproductive failure due to climate change of the anchovy. By providing critical insights into the effects of climate on this key species, independent of fishing pressure, our results may be used to inform and integrate novel policy targets for climate-resilience and to help inform and develop adaptive management strategies that enable a more sustainable exploitation of marine resources (Goh 2012; Queirós et al. 2018).

**Methods**

*The European anchovy study system.* Three stocks over eight in Mediterranean Sea are “currently lying outside safe biological boundaries” *literarily* Vasilakopoulos et al., 2014. To date, management efforts for European anchovy stocks based on long-term monitoring coupled with environmental indices and simulation have proven unsuccessful (Borja et al 1998, Allain et al 2001, Iriarte et al 2002, De Oliveira et al 2005). Management measures of this species have mainly consisted of technical measures such as: the establishment of minimum conservation reference size, catch regulation, limitation of fishing areas, closed seasons and mandated changes in gear size. The harvest control rule drives the ICES advice on setting the Total Allowable Catch (TAC quota; *e.g.* Subarea 8, Bay of Biscay). Therefore, bio-economic simulations performed to assess the biological and economic consequences of a fixed TAC to manage an anchovy stock in Spain (purse seine fleet, Gulf of Cádiz), described this strategy as causing biological and economic vulnerabilities with a consequent fragmentation of sustainability (Ruiz et al. 2017). The same authors explored an adaptive TAC, such an alternative strategy to account for the inherent stock variability and resulting in balancing profits and sustainability. The limits of the classical use of a TAC levels have been underlined by Lehuta et al. (2010), which suggested a more adaptive TAC setting, proportional to recruitment. Interestingly, a sensitivity analysis performed by these Authors confirmed the importance of fecundity for population growth, supporting proposals to protect spawning. The capability to realistically predict spawning in spatially and temporally varying environments has been already highlighted in the Bay of Biscay (Pecquerie et al. 2009). Therefore, such measures cannot yet be applied in annual management cycle due to the difficulty of predicting recruitment that, instead, would require a seasonal-based management (Fréon et al., 2005). Fecundity was recently suggested as reference point to estimate the stock reproductive potential, improving the understanding of stock dynamics and the promotion of fishery-independent data collection (*sensu* Kell et al. 2015).

*The Dynamic Energy Budget (DEB) model.*DEB theory (Kooijman 2010) provides a conceptual and quantitative framework to model metabolism at the whole organism level encompassing all life-stages. The standard DEB model (Kooijman 2010; Sousa et al. 2010; Kearney 2015) describes the rate at which an organism assimilates and utilises energy for maintenance, growth and reproduction as a function of parameters that characterise the species’ physiology and its response to environmental forcing variables (*e.g.* food availability and temperature) taking into account metabolic trade-offs. The model has three state variables: reserves (E), structure (V) and maturity (EH) tracking the development of an individual (see Supporting Information, Table S1). The dynamics of these variables are determined by six energy flows formulated in J d-1: assimilation flow , mobilization flow , somatic maintenance flow , maturity maintenance flow , growth flow , maturation/reproduction flow (see Supporting Information, Figure S1). The model states that energy is assimilated , from food and transferred into reserve (E). According to the κ-rule a fixed energy fraction (κ) is allocated to growth and somatic maintenance, while the remaining fraction (1-κ) is allocated to maturity maintenance plus maturation or reproduction. Changes in environmental conditions (changes in temperature, food availability etc.) thus can be translated into effects on growth and reproduction.

In contrast to net-production models (*e.g.* scope for growth), which assume assimilated energy is partitioned between maintenance and both growth and reproduction, DEB theory assumes assimilated energy is first stored as reserves, and is then distributed among physiological processes (Filgueira et al. 2011). This storage effect permits the exploration of time history effects, specifically those related to energetic status (feeding history) and vulnerability to factors such as temperature (Kearney et al. 2010). DEB represents a reliable and powerful tool to mechanistically describe the whole life cycle of an organism and to make predictions of life-history traits (Pecquerie et al. 2009; Kearney et al. 2010; Pethybridgeet al. 2013; Nisbet et al. 2012). DEB theory therefore allows, through the explicit modelling of energy and mass fluxes through organisms, the derivation of individual performance in terms of the most important life-history traits of a species as maximum length, Lmax, and Total Reproductive Output, TRO (Pecquerie et al. 2009; Kearney et al. 2010; Sarà et al. 2011; 2013a, b; 2014; 2018; Nisbet et al. 2012; Pethybridge et al. 2013; Mangano et al. 2019). DEB also allows an understanding of the interacting time histories of exposures to environmental conditions. Thus, for example, increasing temperature can (up to a point) increase metabolic rates. These in turn can lead to faster rates of maturity (higher TRO values) and growth (higher Lmax values), but only in the presence of sufficient food. In contrast, increased metabolic demand in the absence of food can lead to rapid declines in growth (lower Lmax values).

Aside from the basic assumptions of standard DEB model (*i.e.* one reserve and one structure compartment, isomorphic growth; Kearney 2010) some other supplementary assumptions are needed to account for the specificity of this model. Although the von Bertalanffy growth equation, based on physiological assumptions, is the most commonly used descriptor of indeterminate growth (Charnov 1993), it has been often stated that this equation does not describe larval fish growth unless it is: *i)* an isomorph, *ii)* living in constant environmental conditions, *iii)* with constant surface-area specific searching capabilities for food (Kooijman 2010). Here we assume that the growth of a larvae departs from isomorphic growth and start to growth exponentially with age (V1-morphic) until it reaches puberty. Pethybridge (2013) found that anchovy larvae have different (more cylinder) shape to juveniles and adult, and so estimated the respective shape coefficients. In order to simulate the exponential growth and avoid the effects of abrupt shape changes between life-stages we followed Pethybridge’s (2013) approach allowing the shape coefficient to linearly change with size from day - 0 () until puberty, using the equation

since then the adult shape () was applied.

In our proof-of-concept we decided to present (mapping) and discuss only maximum length (Lmax, cm) and Total Reproductive Output (TRO, the total number of eggs per life span) among all the modelled life-history traits (mapped outcome of “time to catch size”, “eggs” and “reproductive events” are reported into Supporting Information, Figures S4-S6). Lmax and TRO were selected as representing crucial parameters for size-based management and conservation measures (*e.g.* minimum size limits designed to allow individuals to reproduce at least once, maximum allowable catch size, temporal or spatial closure *i.e.* spawning areas, spatial allocation, rotating closure areas, and seasonal-area closures (Stram and Evans, 2009) of designation based on high reproductive output). The knowledge of organismal body temperature (assumed to be similar to Sea Surface Temperature, SST) and environmental food densities are prerequisite, together with the *Engraulis encrasicolus* species-specific DEB parameters (see Supporting Information, Table S2), to run the DEB model.

*Forcing variables: temperature.* Due to the short life span of the anchovy (~4 years), we extracted daily Sea Surface Temperatures (SST; 1 km resolution) from JPL MUR SST data (2010) (<https://podaac.jpl.nasa.gov/Multi-scale_Ultra-high_Resolution_MUR-SST>) over a time range of 4 years (2011-2014) for each cell (see Supporting Information Figure S1). To simulate the effect of future increases in temperature, as forecasted by COP 21 (*sensu* COP 21 Paris Climate Conference Agreement; Hulme 2016) we performed a sensitivity analysis by running DEB models, cell by cell, and by increasing the current temperature from 0.5°C to 2.0°C (0.5°C step) obtaining four increasing temperature DEB scenarios (current + 0.5°C, + 1.0°C, + 1.5°C, + 2.0°C). All simulations were run on an hourly base following the approach of Sarà et al. (2012).

*Forcing variables: food density.* Food availability is an important forcing variable of the model and is expressed as density (wet mass mg m-3), which for anchovy primarily comprise zooplankton (Tudela and Palomera 1997 and references therein). Because locally collected data for zooplankton were spatially and temporally fragmented due to sampling effort, due to this gap of representativeness of the actual food availability for anchovies throughout the study area (Torri et al. 2018), we decided to obtain a spatially continuous dataset on the distribution of food throughout by following the approach proposed by Strömberg et al. (2009) and applied by Mangano et al. (2019). This approach involves transforming weekly Net Primary Productivity (NPP) into wet mass of zooplankton (mg m-3) using the conversion coefficient provided by the ICES Committee on Terms and Equivalents (Cushing 1958) starting from NPP values of carbon *per* unit volume expressed as grams of carbon/meter3/day. The NPP dataset was obtained from Oregon State University (2017), values were extracted for each cell (0.11°x 0.11° [~12.5 km2]) over a time span of 4 years (2011 – 2014) to reflect the short life span of the anchovy (see Supporting Information Figure S2). To simulate future trophic changes, we carried out a sensitivity analysis by adding or subtracting (cell by cell) a fixed amount of 10% generating three future scenarios: oligotrophic (current NPP - 10%), eutrophic (current + 10%) and no-change (current NPP).

*Model outcomes validation.* DEB Lmax simulation have been validated by extracting data from the retrieved literature after having search using a complex search string combining prominent or substantial key-words [((“*Engraulis encrasicolus*” OR “European anchovy”) AND (“Total length” OR “Maximum length” OR “length” OR “size class” OR “length-weight" OR “age” OR “life stage”) AND “Mediterranean sea”)]. The search string was entered into scientific computerised databases such as: ISI Web of Sciences and Scopus. A hand search was also performed on the bibliographies of relevant review articles to identify any additional references. The “all years” timespan was selected during the search. Searches were confined to English language; only titles, abstracts and keywords were searched by. Data have been extracted from Basilone et al (2004, 2006) and fitted on an observed vs predicted model regression (Figure 1, upper panel). DEB TRO simulation outputs were validated using *in situ* data collected during *ad-hoc* oceanographic surveys, “Bansic” cruise. Anchovy eggs data used to validate the model have been collected during five summer surveys on board the R/V “Urania” for each year comprised over the period 2006-2010, approximately in correspondence with the peak of reproductive period for anchovy in the study area (Tsikliras et al., 2010). The systematic sampling is constituted by a regular grid of stations (1/10°×1/10° along the continental shelf, and 1/5°×1/5° further offshore). Planktonic sampling was conducted day-night independently by using oblique tows with a Bongo 40 net (two mouths of 40 cm inlet diameter, 200 μm mesh). The plankton oblique tows were carried out from within 5 m from the bottom to the surface in “shallow” stations (bottom depth < 100 m), or from 100 m depth to the surface in deeper stations, wherever possible, with a constant speed of 2 knots. In each mouth, calibrated flow-meters were mounted in order to calculate the volume of filtered water (m3). Samples were preserved using a borax-buffered solution of 4% formaldehyde and seawater. In order to identify eggs of European anchovy, all samples were observed under a microscope once in laboratory and fish eggs were sorted from the rest of the plankton and identified according to Whitehead et al. (1988). The number of eggs, collected at each station, was normalized as

Yi = (di× xi) / vi ,

where Yi is the number of anchovy eggs under one m2 of sea surface at station i, xi is the number of eggs taken at station *i*, vi is the volume of water filtered in m3 and di is the maximum depth (in meters) reached by the net. A total of 379 stations from five years of survey were included in the observed vs predicted model regression (Figure 1 lower panel). Both model output (Lmax and TRO) predictions were tested against observations at specific times and places (*ad hoc* DEB models have been runned for those same places based on environmental conditions).

*Model outcomes mapping.* We performed simulations to investigate potential variations in the maximum length and fecundity of *Engraulis encrasicolus* under different climate and food availability scenarios. Model outputs are expressed in terms of maximum length (Lmax, cm) and Total Reproductive Output (TRO, the total number of eggs per life span) and presented through climate informed scenario-based quantitative maps (Figures 2, 3), minimum, maximum, mean and median values for each scenario are also reported. The differences between scenarios temperature and food have been mapped and reported for both Lmax and TRO (Figures 4, 5). All spatial analyses were performed using GIS procedures and tools, specifically ESRI ArcGIS 10.2 (and Spatial Analyst extension) and R software (R Core Team, 2019), then represented through the ggplot2 package (Wickham, 2016). Our simulations were restricted to the continental shelf on the basis of depth (from 0 to 200 meters below sea level) identified through bathymetry data obtained from EMODnet (2016). A vector polygon grid feature class of 346 square cells (having a size of 0.11° x 0.11° [~12.5 km2]) covering the study area was used.

To analyse the spatial distributions and trends of both Lmax and TRO patches, under the selected scenarios, *z*-score values and strength of clustering (positive = high clustering; zero no apparent clustering; negative = low clustering) were estimated through the Spatial Analyst tool of ArcGIS (Getis and Ord 1992; Getis 1993) and reported for each scenario and life-history trait respectively (only significant, p < 0.05, values are reported). G statistics allows to evaluate the spatial association of a variable within a specified distance of a single point., here we used global G statistic G(*d*), which measures overall concentration or lack of concentration of all pairs of (xi, xj) such that i and j are within *d* (a given distance) of each other, giving us an information about high or low, positive or negative, spatial clustering of variables. The distance *d* in km has been set reasonably at 25 km, the double of the minimum distance between two cells, given the resolutions of the map, in order to consider, for each cell, the two neighbouring cells in each direction. G(*d*) has been chosen as apply on non-regular grid (as in our case). Relating to quantiles of standard normal distribution, high negative or positive values of G statistic mean that there i clustering tendency of, respectively, low and high values of the variable. Values of G(*d*) near to zero indicate a not significant clustering tendency, generally visualized as a flat spatial pattern.

**Results**

DEB model outputs based on observed environmental conditions provided good predictions of the two selected life-history traits in European anchovy, giving a high level of confidence in the generated forecasts (Figure 1, model validation). Validated DEB model outcomes of both the proxy of population size-structure (maxL) and proxy of population fecundity (TRO) across the study area were positively affected by increased temperatures (see scenarios-based quantitative map, Figures 2, 3 central panel, resulting outputs from current temperature to +2 °C scenario with + 0.5 increment intermediate scenarios) coupled with increases in trophic conditions (see scenarios-based quantitative map; Figures 2, 3 right panel, eutrophic condition +10% of net primary production). An increase in food availability had a greater effect on both life-history traits, with the highest mean values being predicted under the higher food (eutrophic) scenario (*i.e.* 10% above current levels of nutrients. Scenario-based quantitative maps of life-history traits represent the geographically explicit forecasts across the study area (model predictions in each cell; Figures 2, 3). The size structure (Figures 2, 4) and the fecundity (Figures 3, 5) of the anchovy will shift under future conditions with scenario specific response patterns.

*Growth patterns (Lmax).* Generally, increasing temperatures promoted the spatial extension of the highest Lmax values (Figure 2)Temperature increases under oligotrophic conditions led to a decrease in the spatial extent of the largest anchovies, whereas eutrophic conditions facilitated an increase (Figure 2). Anchovies were predicted to never achieve the maximum size under temperature increase scenarios coupled with oligotrophic conditions (. Under the highest temperature scenario, +2°C, coupled with oligotrophic conditions, the anchovies will reach the lower value of Lmax (maximum size = 13.62 cm, minimum size 11.81 cm; Figure 4).. Under eutrophic conditions the species will achieve the higher value of Lmax recorded by the model (15.56 cm) at the highest temperature increase (+2°C; Figure 4)

*Fecundity patterns (TRO).* A similar spatial heterogeneity characterised the TRO simulated responses, the model identified areas predicted to be more productive (Figure 3, highest values, darker colours) and a loss of productivity (Figure 3, grey colour), with highest percentage of loss under oligotrophic food condition (-10% NPP), ranging respectively from the 33% of loss under current temperature and 24% under the maximum exploited temperature scenario, +2°C. Lowest percentages of reproductive failure were recorded under eutrophic food condition (+10% NPP) ranging from a maximum percentage of loss of 11% under current temperature and a minimum of 8% under the maximum exploited temperature scenario, +2°C (Figure 3, grey colour). Differences among crossed scenarios showed increase of TRO under increased condition of temperature and food (Figure 5, green colour, left panel.

According to G statistics and their respective *p*-values reported in each map (Figures 2-5), the spatial analysis of patchiness among all life-history traits of the European anchovy a significant tendency to cluster higher values of TRO and a non-significant tendency to cluster values of TL, along all trophic and temperature scenarios.

**Discussions**

The mechanistic approach applied in our proof-of-concept, using DEB theory, allowed for a comparison of current baseline conditions of European anchovy life-history traits distribution against those that can be expected under future climate scenarios. The present model provides highly reliable, quantitative, spatially-explicit predictions of how changes in climate-related environmental conditions will potentially affect life-history traits such as growth (Lmax) and reproduction (TRO). These traits were selected as they drive population dynamics and represent essential information for managing commercially important species both currently and in the future (Queirós et al. 2018). Our approach generates spatial forecast data with a previously unachievable fine-scale (~12.5 km) resolution, allowing the identification of threats and opportunities for the long-term sustainability of the commercially important anchovy, with implications for the European anchovy fisheries sector. The presented approach has a potential wide range of applications to fisheries stocks globally, assisting in the implementation of existing management evaluation strategies and helping to develop more climate-resilient, trans-boundary resource management planning options.

*Fecundity as an early warning proxy of species vulnerability: a baseline tool to formulate control measures*. As the first input-driver of a species’ population dynamics, fecundity can be coupled with Lagrangian physical-biological models to predict species local persistence over time, source areas, and dispersal over time, sink areas, at fine spatial resolution (Falcini et al. 2015; Politikos et al. 2015). Persistence is an essential component of predictive forecasts of future status of commercial stocks and one of the most important population traits for the efficient creation of climate-driven adaptive management plans (Munroe et al. 2012; Holsman et al. 2019). In this context the scenario-based forecasts of size and productivity shifts for target species, such as the European anchovy, can be used to address the development of seasonal (or even higher such as monthly), adaptive TAC, proportional to life-history traits. By our TRO outcomes we may help in improving the degree of accuracy when performing modeling exercise to evaluate strategies and the robustness of management options. Interestingly, our approach, although applied in a limited geographic region, demonstrates new capabilities for predicting areas of future species vulnerability in terms of changes in spatial connectivity (patchiness) and increase/decrease of reproductive failure (Montalto et al. 2016). Quantitative information on fragmentation of spawning areas, *i.e.* more productive patches, recognized as Essential Fish Habitat (EFH, *sensu* Benaka 1999), fills a critical knowledge gap regarding the capacity to implement spatially-explicit management strategies. It also facilitates the design of tailored temporal and/or spatial mitigation measures of fisheries pressures *i.e.* control provision measures such as special rules concerning fishing permits in specific areas allowing to plan the fishing fleet capacity over long time temporal scale, the design of protection areas within or between reproductive patches of higher productivity that represent source populations for the neighboring areas (e.g. spawning), which can be used to increase stock resilience. As a proxy for recruitment variability, predicted fecundity can represent an effective metric for defining sustainable exploitation strategies (Shelton et al. 2014).

*Spatial explicit identification of source areas: a baseline tool to address protection and adaptation measures.* The need to increase knowledge of population shifts of this species is also crucial because anchovy is the most common forage fish eaten by large predators in the Mediterranean Sea, including Atlantic Bluefin tuna and European hake (Olson et al., 2016). Detecting shifts in the anchovy population can provide a means of foreseeing and disentangling interconnected responses within the multiple hierarchical levels of the food web that this species sustains. The scenario-based quantitative maps resulting from our proof-of-concept clearly identified source areas (Lewin 1989) where anchovy will still be capable of reproducing under the worst foreseen conditions, and therefore serve as “rescue sites” (Assis et al. 2017). The number, distribution and extent of source areas could provide the most reliable baseline information for identifying and prioritizing areas for protection (*e.g.* no-take areas; Giannoulaki et al. 2013). Other sites may in contrast serve as sinks where fish are able to rapidly grow, but may fail to reproduce. Recent models of the effects of Marine Protected Areas on anchovy stocks in the Bay of Biscay, Lehuta et al. (2010) have emphasized high uncertainty in the values of mortality of larvae and juveniles, growth, and reproduction, all gaps that invalidate the effectiveness of the simulated MPA designs. The localization of areas of highest productivity coupled with other factors, including local and regional oceanography (Falcini et al. 2015; Politikos et al. 2015), can allow identification of sink areas forecast under future climatic scenarios and can be useful to redirect research and management strategies. This knowledge is essential for an effective and successful adaptive management of exploitation by fishing activities and for the maintenance and enhancement of climate-resilience in the context of marine resources management (Pikitch et al. 2004; Berkes 2012; Lawler et al., 2010; Noble et al., 2014; Pinsky and Mantua, 2014; Busch et al., 2016; Costello et al., 2016).

Our scenario-based quantitative maps are expected to improve our ability to cope with expected changes in fishery practices at sea (*e.g.* fleet behaviour shifts) and to better manage the relocation of human activities (*e.g.* fish farms, wind farms) and the enactment of an efficient maritime spatial planning (Domínguez-Tejo et al. 2016). Fishery-dependent communities along cross-border coastal areas could be offered the opportunity to maximize their adaptive capacity and minimize their socio-economic vulnerability (*i.e.* climate-proofing for development) with a general improvement of social-ecological system resilience to environmental changes (Folke 2006; Liu et al., 2007; Charles, 2012; Lubchenco et al., 2016; Holsman et al., 2019).

Instead of long-term and fixed solutions, more flexible, tailored and adaptive tools and strategies would facilitate the implementation of fisheries management plans that incorporate the recovery of populations overfished or threatened by stressors with both local (*e.g.* pollution) and global origins (Folke 2006; Halpern et al. 2008; King et al. 2015; Queirós et al. 2018). Mechanistically-based forecasts can help to promote more flexible management plans based on a system of year-by-year assessment of marine resources (*i.e.* based on seasonal assessments and revision of benchmarks and protection, adaptation, mitigation management options) and facilitate more appropriate and specifically tailored monitoring plans.

*Model key assumptions.*

**Conclusion**

The approach proposed by our proof-of-concept addresses environmental changes, and the resulting mapped outputs built on climate uncertainty, may represent a tool to enhance ecological resilience under climate change supporting a more adaptive fisheries management. The explorative sensitivity scenarios projections was confirmed as powerful tool to scope biological responses. Our approach represents a robust tool (as tested against a wide range of climate scenarios), flexible, integrative and responsive to feedback and learning (more external drivers may be integrated), efficient (outputs implementation into an adaptive management may increase management benefits and reduced costs; *sensu* Nobles et al. 2014) over which build a climate-resilient, adaptive, management (*sensu* Holsman et al. 2019) designed to support the long-term sustainability of fishery resources. The future coupling with other analytical tools (e.g. physical and topographic barriers; Bacha et al., 2014; or food web models) could provide a promising approach towards the implementation of Ecosystem Based Management within the context of global change.

Waiting for the next policy window (sensu Rose et al. 2017), technically a windows of opportunity for policy change requiring uptake of knowledge, even when it has been previously ignored; this study reinforces the growing chorus of scientific literature and scientists calling for a more “ecologically sound” reframing of management areas established based on political and statistical considerations by the Scientific Advisory Committee of the GFCM (GFCM, 2012), which otherwise risk being invalidated, threatening the effectiveness of the enormous efforts which now proliferate in current management policies.

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**Author Contributions**: GS conceived the idea and the modelling design with the contribution of MCM; MCM performed the systematic review to set-up the modelling exercise and lead the writing; FF, AG and BP provided data and useful feedback in data interpretation; AG performed the DEB modelling analyses and TD and TS the fine tuning of DEB writing; GB and GB performed environmental data gathering, G.I.S. data analysis and mapping; AC and BP provided the dataset for model validation; MCM, GS, NM, FP, MJ, GAW and BH wrote the manuscript; all authors reviewed and commented on final manuscript; GAW, SM and GS provided research funds and facilities.

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**Figure captions**

**Figure 1. Model validation.** Regression lines between observed and predicted data, equation and significant values are reported. Upper panel, Lmax outputs simulations validated by using data extracted from literature (Basilone et al. 2004; 2006). Lower panel, TRO outputs simulations validated by using data collected *in situ* (*ad-hoc* oceanographic surveys conducted in the framework of various national projects - RITMARE project, FAO MedSudMed GCP/RER/010/ITA - as well as in the framework of more regional projects funded by Ministero dell’Innovazione, Ministero Ambiente, Regione Sicilia; as from Patti et al. 2017).

**Figure 2.** Scenarios-based quantitative maps of Maximum length (Lmax, cm) described by a continuous scale ranging (from 0 to 16) under current conditions of both temperature and food (central panel) and under four increasing temperature scenarios (+ 0.5; + 1.0; + 1.5; + 2.0 °C) coupled with decreasing (oligotrophic, - 10% net primary production, left panel) and increasing trophic conditions (eutrophic +10% net primary production, right panel). Minimum, maximum, mean and median values for each scenario have been also reported inside each map as well as the global G statistic values. Total number of cells = 346, cells resolution of 12.5 x 12.5 km2. Maps were created using R software (ggplot2 package).

**Figure 3.** Scenarios-based quantitative maps of Total Reproductive Output (TRO, n. eggs / n. of reproductive events) described by a continuous scale ranging (from 0 to 1,400,000) under current conditions of both temperature and food (central panel) and under four increasing temperature scenarios (+ 0.5; + 1.0; + 1.5; + 2.0 °C) coupled with decreasing (oligotrophic, - 10% net primary production, left panel) and increasing trophic conditions (eutrophic +10% net primary production, right panel). Minimum, maximum, mean and median values for each scenario have been also reported inside each map as well as the global G statistic values. Total number of cells = 346, cells resolution of 12.5 x 12.5 km2. Maps were created using R software (ggplot2 package).

**Figure 4.** Scenarios-based quantitative maps showing differences between Maximum length (TLmax, cm) described by a continuous scale (from -0.48 to 0.46) respectively across the examined temperature scenarios (central panel, current temperature *vs* all the four temperature increasing scenarios of +0.5°C increase up to +2 °C). Differences between current primary production food condition and oligotrophic, - 10%, food condition *per* each temperature scenarios (+ 0.5; + 1.0; + 1.5; + 2.0 °C, left panel). Differences between current primary production food condition and eutrophic, +10%, food condition *per* each temperature scenarios (right panel). Minimum, maximum, mean and median values for each scenario have been also reported inside each map as well as the global G statistic values. Total number of cells = 346, cells resolution of 12.5 x 12.5 km2. Maps were created using R software (ggplot2 package).

**Figure 5.** Scenarios-based quantitative maps showing differences between Total Reproductive Output (TRO, n. eggs / n. of reproductive events) described by a continuous scale (from -562,550 to 577,740) respectively across the examined temperature scenarios (central panel, current temperature *vs* all the four temperature increasing scenarios of +0.5°C increase up to +2 °C). Differences between current primary production food condition and oligotrophic, - 10%, food condition *per* each temperature scenarios (+ 0.5; + 1.0; + 1.5; + 2.0 °C, left panel). Differences between current primary production food condition and eutrophic, +10%, food condition *per* each temperature scenarios (right panel). Minimum, maximum, mean and median values for each scenario have been also reported inside each map as well as the global G statistic values. Total number of cells = 346, cells resolution of 12.5 x 12.5 km2. Maps were created using R software (ggplot2 package).